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and simultaneous autoregressive models. At the global scale, we found a close relationship between herb species richness and temperature parameters, with no differences between continents. The subdivision into three main taxonomic groups (ferns, monocots, dicots) showed that each group has distinct relations to environmental factors and differences in richness between continents. Most of the 72 families found have pantropical distributions but 12, 11, and 16 families were significantly over-represented in America, Africa, and Asia, respectively. Although total species richness was closely related to climatic factors, ferns, monocots and dicots were represented by distinct sets of families with varying species richness on each continent. Which species are found at a given site may thus reflect group-specific evolutionary and historical factors.

Keywords Species richness · Terrestrial herbs · Tropical rainforest · Vascular plants · America · Africa · Asia · Climate

Introduction

Tropical rain forests are the most species-rich terrestrial ecosystems (Primack and Corlett 2005). The causes leading to this high species richness are still incompletely understood and likely involve a combination of environmental and evolutionary factors (Hill and Hill 2001). For example, a significant number of studies have documented the fact that the species richness of both animals and plants in tropical forests are associated with broad- and mesoscale temperature gradients and other environmental variables (e.g., Hawkins et al. 2003; Kreft and Jetz 2007; Field et al. 2008). Energy and water availability may constrain the number of species that can coexist in a region and their capability to adapt to colder and drier climates (Hawkins et al. 2003; Currie et al. 2004; Wiens and Donoghue 2004). Topography and habitat heterogeneity may also influence local species richness, determining the number of niches and hence of species that can co-occur while possibly also influencing speciation rates (Kerr and Parker 1997; Ricklefs 2004). Contemporary environmental conditions thus appear to constrain regional species richness (Hawkins et al. 2003; Field et al. 2008), and different plant groups respond differently to the same environmental variables (Kreft et al. 2010; Ricklefs and Renner 2012). On the other hand, there is increasing evidence that the number of species in tropical regions is influenced by evolutionary constraints and historical factors such as past climatic fluctuations (e.g., Wiens and Donoghue 2004; Kissling et al. 2012).

Plant diversity is unevenly distributed between tropical regions, with tropical America approximately 93,500 plant species being the most species rich continent followed by Asia and Africa with 62,000 and 20,000 species, respectively (Primack and Corlett 2005). These differences are often attributed to different impact of past climatic fluctuations and contrasting developments in the extent of tropical rain forests over time (Kissling et al. 2012). On the other hand, the largely independent evolutionary histories of tropical biomes on the three major geographical landmasses have allowed for idiosyncratic developments whose comparisons can provide important insights into the factors determining the diversity and composition of biotic assemblages (Corlett and Primack 2006; Ricklefs and Renner 2012). At the same time, there is marked local, regional, and intercontinental variation in the diversity and taxonomic composition of these forests (Corlett and Primack 2006). For example, in Ecuadorian Amazonia about 1,000 vascular plant species have been recorded on a single hectare (Balslev et al. 1998) while in about 300–400 species are found on the same surface area (Linares-Palomino et al. 2009). Spatial variability of species numbers

and composition has been widely documented for trees (e.g., Gentry 1988; Pitman et al. 2008; Ricklefs and Renner 2012), but is less well known for other life forms.

Despite the ecological importance that trees play in tropical ecosystems, the majority of vascular plant species in tropical forests belong to other life forms (Gentry and Dodson 1987; Balslev et al. 1998; Linares-Palomino et al. 2009). Depending on forest type and ecological conditions, the relative contribution of understory herbs, shrubs, lianas and epiphytes varies considerably (Wolf and Alejandro 2003; Linares-Palomino and Kessler 2009). The understory in tropical forest is often constituted by trees seedling while herbaceous species are less abundant (Richards 1996). Yet, understory herbs can represent about 45 % of the vascular plant diversity in tropical forests (Gentry and Dodson 1987; Balslev et al. 1998; Linares-Palomino et al. 2009). Although there are numerous studies focussing on the variation of species richness and community composition of tropical forest herbs at local to regional scales (e.g., Poulsen and Balslev 1991; Kelly et al. 1994; Poulsen and Pendry 1995; Annaselvan and Parthasarathy 1999; Chittibabu and Parthsarathy 2000; Costa 2004; Costa et al. 2005; Poulsen et al. 2005, 2006; Linares-Palomino et al. 2009), an intercontinental comparison is lacking to date.

In addition to their life form, understory herbs differ in numerous other ways from trees. Thus, understory herbs are often rather unevenly distributed on the tropical forest ground, and species with underground rhizomes or stolons are frequent (Richards 1996). There are numerous examples of social species forming dense patches of several square metres, such as Melastomataceae in tropical America, grasses in Africa, and Melastomataceae and Zingiberaceae in Malayan forest (Richards 1996). Further, while the majority of tropical rainforest trees belongs to the dicotyledonous angiosperms (dicots), among the understory herbs, monocotyledons (monocots) as well as ferns and ferns allies (henceforth called ferns for simplicity) are also prominent. These three major groups differ markedly in their physiological and morphological adaptations. For example, monocots typically have diffuse root systems without one or few dominant roots as found in most dicots. These different architectures affect the way in which the plants absorb nutrients and water (Robinson 1994). On the other hand, ferns have different stomatal control and lower water use efficiency than angiosperms (MacAdam and Brodribb 2012) so that they are mostly shade-demanding and increase in abundance in particularly damp and shady places, such stream and valleys (Bhattarai et al. 2004; Kessler et al. 2011; Kluge and Kessler 2011). Ferns were long considering as being evolutionary leftovers from the Palaeozoic and Mesozoic era (Niklaus et al. 1983) but recent research has shown that the extant diversity of ferns resulted from a more recent diversification trailing the rise of angiosperms (Schneider et al. 2004). Finally, while seed plants have a wide range of dispersal strategies involving, among others, animals, water, and wind (Zomlefer 1994), ferns are only wind dispersed. This allows ferns to colonize new environment easily so that oceanic island have overall more species but a lower number of endemic species than seed plant species (Moran and Smith 2001; Kreft et al. 2010).

In this study, we analysed the patterns of diversity of understory herbs in American, African, and Asian tropical forests and contrast the patterns of ferns, monocots, and dicots. Specifically, we asked the following questions: (1) how is the richness of understory herb assemblages correlated to climatic factors? (2) Are there differences in the species richness and taxonomic composition of understory herb assemblages between the three continents? (3) Are there differences between the three main taxonomic groups (ferns, monocots, dicots) with respect to their environmental relationships as well as between continents?

Materials and methods

Study areas

Our sampling was aimed at accumulating the largest possible number of samples from as many locations and tropical forest habitats as possible. Sampling was mostly conducted on the side within the scope of other research projects and the location of study sites did not follow a specific design. Study sites covered three countries in the Neotropics [Mexico (4 transects), Costa Rica (5), Bolivia (14)], three in Africa [Uganda (12), Congo (4), the oceanic island of La Réunion belonging to France (4)], and two in Southeast Asia [Malaysia (4), Indonesia with the islands of Borneo (6), Sulawesi (22) and Bali (5)] (Fig. 1).

Field work was conducted in 1994–1999 in Uganda and Congo and in 2007 and 2008 at the remaining sites. The elevational range, equally distributed among the three areas, ranged from 50 to 2,300 m while mean annual precipitation ranged from 733 to 4,360 mm (Table 1). After an initial survey of a prospective location, study sites were selected according the following criteria in order to be comparable: (1) mature forests, (2) forest structure and canopy cover were visually representative of the regional forests, (3) avoiding special microhabitat such as water-logged soils or open rock faces, (4) minimum distance of 150 m from the forest edge to avoid edge effects, (5) orography with low inclination to avoid steep forest exposition and canopy openness and (6) we tried to have sites with a mean annual precipitation well over 1,000 m, except two Bolivian sites.

Field sampling and environmental factors

We defined understory herbaceous plants following Poulsen (1996) as non-woody or only slightly woody plants that are rooted on the forest floor, including facultative terrestrial species like epiphytes that are only at ground level for part of their life cycle. All herbs recorded on each study transect were sorted to morpho-species and determined to family level.

We recorded all understory herbs on 86 transects of 445 m each. We established 1 to 9 (mean = 3.7) transects per site (Table 1). Each transect consisted of a line of 12 plots of 5 m × 5 m each, separated by 35 m from each other. This method allowed us to assess herb diversity at two spatial scales: the 5 × 5 m plot (plot scale) gives an indication of the

Fig. 1 Location of the study sites indicating the number of transects sampled

Table 1 Summary table of the study sites

Countries	Transects	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Coordinates	
Mexico Veracruz (Los Tuxtlas)	2	250	24.5	3,507	18°35′12.4″N	95°04′39.6″W
Mexico Veracruz (Rancho Don Alfonso)	2	1,670	16.8	1,925	19°31′00.3″N	97°00′28.2″W
Costa Rica (Reserva de Vida Silvestre Golfito)	4	50	26	4,360	8°38′19.6″N	83°10′00.0″W
Costa Rica (La Selva)	1	50	26	4,000		
Bolivia (Río Seco)	4	392	24.1	1,085	18°42′53.6″S	63°11′31.6″W
Bolivia (Santa Cruz)	4	400	24.9	3,710	17°46′54.3″S	63°03′59.5″W
Bolivia (Buena Vista)	4	425	24.3	733	17°30′57.4″S	63°38′07.1″W
Bolivia (Villa Tunari)	2	400	24.9	3,710	16°57′59.2″S	65°24′44.5″W
Uganda (Kasyoha)	3	1,325	23.1	1,375	0°25′S	30°20′E
Uganda (Kibale)	3	1,445	22.2	1,500	0°40′N	30°35′E
Uganda (Budongo)	6	1,445	22.2	1,500	1°55′N	31°46′E
Congo (Ituri)	4	800	24.2	1,672	1°19′06.7″N	28°38′41.2″E
La Réunion (Mare Longue)	2	250	22.3	4,000	21°10′56.5″S	55°21′48.5″E
La Réunion (Foret de Bebour)	2	1,350	16.1	3,000	21°07′56.5″S	55°34′03.3″E
Malaysia (Taman Negara National Park)	6	200	25.9	2,470	4°23′19.0″N	102°24′0.6″E
Malaysia (Fraser's Hill)	4	1,300	20	2,660	3°42′49.2″N	101°44′12.3″E
Indonesia, Bali (Bedugul)	2	600	23.3	1,978	8°16′45.1″S	115°10′59.9″E
Indonesia, Bali (Barat National Park)	3	1,500	17.8	2,500	8°08′14.1″S	114°28′28.2″E
Indonesia, Kalimantan (Kutai National Park)	4	300	26.6	1,916	0°31′42.3″N	117°28′48.0″E

Table 1 continued

Countries	Transects	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Coordinates	
Indonesia, Kalimantan (Bukit Bankirai)	2	600	26.2	2,304	0°59′32.4″S	116°53′32.4″E
Indonesia, Sulawesi (LLNP, Saluki)	3	250	27.36	1,129	1°17′47.1″S	119°58′30.6″E
Indonesia, Sulawesi (LLNP, Pono valley)	6	1,000	23.44	1,800	1°29′24.2″S	120°3′37.1″E
Indonesia, Sulawesi (LLNP, Bariri)	6	1,400	19.56	1,850	1°39′28.9″S	120°10′3″E
Indonesia, Sulawesi (LLNP, Nokilalaki)	3	1,800	16.8	1,726	1°14′36.7″S	120°9′5.2″E
Indonesia, Sulawesi (LLNP, Rorekatimbu)	4	2,300	15.2	1,726	1°16′43.2″S	120°18′34.3″E

LLNP Lore Lindu National Park

number of species that directly co-occur and potentially interact. In contrast, the combination of the 12 plots along a transect (transect scale) includes species that do not directly co-occur provides an approximation of the total number of herb species in a forest site. At two Indonesian sites where we have complete herb inventories of 1 km^2 of forest (Cicuzza et al. 2010), each transect included 19–32 % of the total herb richness, while three transects combined included roughly 50 %.

For the analyses, we combined the species for a total number and also separated them into three main groups: ferns, monocots, and dicots.

Species richness was correlated to six environmental factors that have previously been shown to closely correlate to plant species richness (e.g., Tuomisto et al. 2003; Kreft and Jetz 2007): elevation, actual evapotranspiration (AET), mean annual temperature, minimum temperature of the coldest month, mean annual precipitation, and precipitation of the driest month. Elevation was recorded on-site with a hand-held altimeter or GPS. AET was calculated using Turc's formula, where $AET = P/[0.9 + (P^2/L^2)]1/2$, with $L = 300 + 25T + 0.05T^3$, P = annual precipitation, and T = mean annual temperature (Turc 1954; González-Espinosa et al. 2004). The climatic factors were extracted from the *WorldClim* model (http://www.worldclim.org/) (Hijmans et al. 2004). We did not include all 19 climatic variables provided by *WorldClim* because this would have greatly inflated the number of variables relative to that of sampling sites and because many climatic variables are highly correlated to each other. In addition to annual mean, we included a measure of seasonal aridity (precipitation of the driest month) and of seasonal low temperatures (minimum temperature

of the coldest month) because limited water availability and low temperatures are well known to be related to the diversity of plants and other organisms (Kreft and Jetz 2007; Hawkins et al. 2003).

Statistical analyses

We analysed species richness at three different levels: plot, transect and beta diversity. Plot diversity was calculated by averaging the values of each 5 × 5 m of each transect. Transect diversity was assessed by summing up the averaged value of species across all 12 plots. In addition we used a measure of beta diversity by dividing the total number of species per transect by the average number of species per plot (true beta diversity following Tuomisto 2010). Moreover, continents were included in the analysis to highlight the difference of families among the three continents. Prior to further analyses, we checked data for homogeneity of variances and considered whether there were linear or non-linear relationships between variables.

We used linear and non-linear regression analyses between plot diversity and transect diversity, plot diversity and beta diversity, and between transect and beta diversity to assess the relationships between these measures of diversity. Moreover, in order to assess any correlations among the environmental variables includes in our analysis, correlation analyses were conducted between all the variables; factors with a r value superior to 0.7 or inferior to −0.7 were included in a Principal component analysis (PCA), in order to reduce the number of variables correlated among each other.

Then, we used backward stepwise multiple linear regression analysis to select the combination of explanatory variables that together best account for herb species richness. The goodness of fit in relation to the model complexity was evaluated by using the Akaike information criterion (AIC), which incorporates the maximized log-likelihood of the model and a term that penalizes models with greater complexity (Johnson and Omland 2004). Model selection was then based on ΔAIC, which is the difference between the AIC values of the model of interest and the AIC of the best fitting model (Johnson and Omland 2004). Because spatial autocorrelation violates the assumption of independently distributed errors in regression models, type I errors of traditional tests might be inflated (Legendre 1993). To explore the influence of spatial autocorrelation between the plots we calculated the Moran's I value of the residual of our minimal adequate ordinary least squares regression (OLS) models. Spatial autocorrelation was then included in simultaneous autoregressive (SAR) models that increase the standard linear regression model with an additional term that incorporates the spatial autocorrelation structure of a given dataset (Arbia et al. 2003). The additional term is implemented with a 'spatial weight matrix' where the neighbourhood of each location (lag distance of d = 10 m) and the weight of each neighbour need to be defined. The spatial weights matrix in SAR models thus accounts for patterns in the response variable that are not predicted by explanatory variables, but are instead related to values in neighbouring locations. Finally, because similar patterns of spatial autocorrelation in the patterns of diversity and the explanatory variables may lead to spurious correlations, we also assessed whether there were purely spatial signals in the diversity data.

Analyses of the family composition of the herb assemblages were conducted using non-metric multidimensional scaling (NMDS), first including all families and then also separately for ferns, monocots and dicots. Furthermore, to identify the families which play a major role on specific continents, we used the Indicator Species Analysis (Dufrene and Legendre 1997).

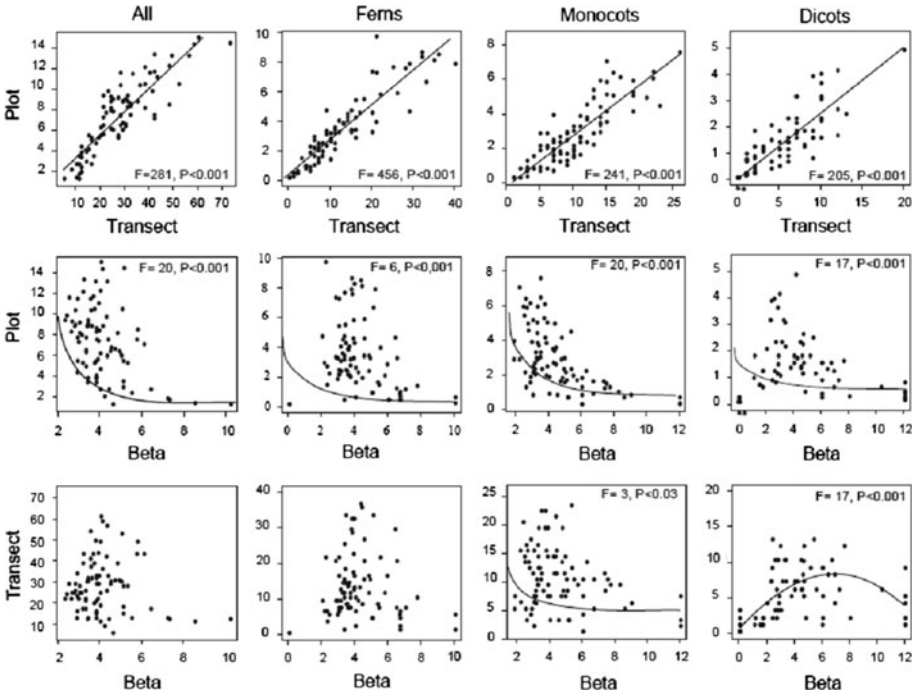

Fig. 2 Relationships between plot, transect and beta diversity of herbaceous species and separately for the three major taxonomic groups. *Lines* depict significant regression relationships

All analyses were conducted with R version 2.10 (R Development Core Team 2008), with additional functions provided by the R package vegan (Oksanen et al. 2007). The Indicator Species Analysis was performed with PCOrd 5.0 (McCune and Mefford 1999).

Results

Within the 23 study sites, we recorded a total of 72 families, 25 belong to ferns, 29 to the dicots and 18 to the monocots. At the continental level, the proportion changed, with America having a total of 53 families including 19 fern, 20 dicots and 14 monocot families. Africa had 35 families in total, with 12 fern, 14 dicot and 9 monocot families. Asia had 50 families in total, with 23 fern, 17 dicot and 10 monocot families.

The 23 study sites with 86 transect (1,032 plots) included in our analysis were unequally distributed among the three major tropical regions (Table 1). South East Asia had the largest number of transects (43), followed by America (23) and Africa (20). Spatial grain size influence patterns of diversity especially when comparing different life forms across different biomes, e.g., herbs in Greenland versus trees in Amazonia. The comparison of a single life form within tropical rain forests, gives us the confidence that local richness would not have a different pattern if we chose a different sampling method. Study on ferns diversity has shown that elevational patterns are highly congruent from local to regional scales (Karger et al. 2011). Species richness per transect ranged from a minimum of 5

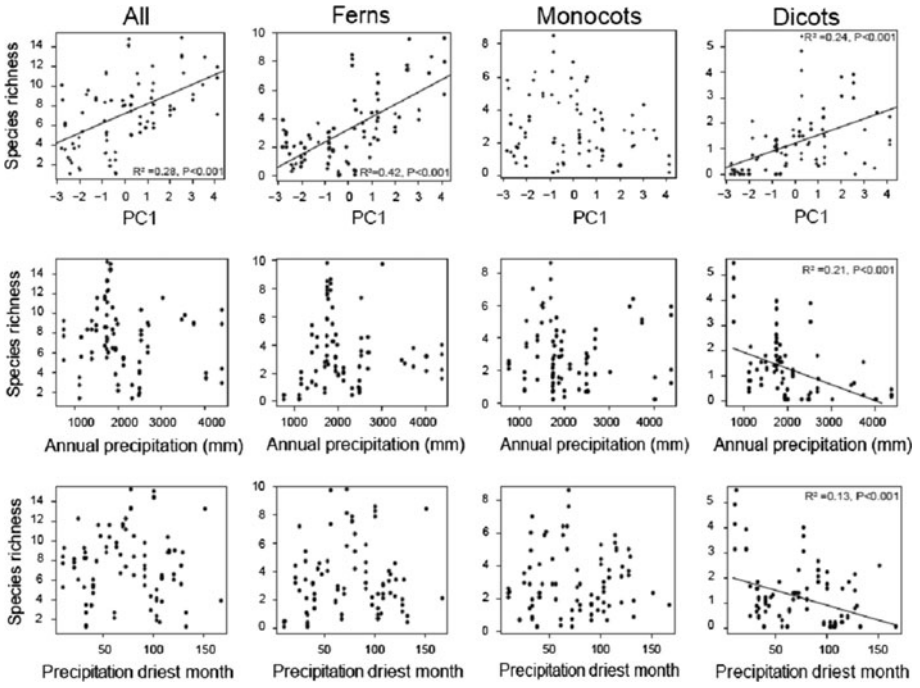

Fig. 3 Regression relationships between the mean number of herb species per plot (25 m^2) and the six environmental factors included in the analyses

along a lowland transect on Borneo to a maximum of 73 species on a transect at 1,000 m on Sulawesi. Average numbers of species per plot ranged from 1 to 15.

The regression analysis between plots and transects diversity recovered significant and strongly positive relationships for all the herbs species and for the three major taxonomic groups (Fig. 2). Plot and beta diversity showed a negative relationship for all groups. Transect diversity and beta diversity were negatively related with monocot richness and showed a hump-shaped relationship with dicots.

The regression analysis among the different factors considered in our analysis recovered *r* values superior to 0.7 between the AET, elevation, and minimum temperature of coldest month. The principal component analysis for these three factors summarized them on the first axis including 71 % of the variance. In all further analyses, we used the PC1 axis values as a compound factors including elevation and factors correlated with it.

Considering the pair-wise relationships of herb diversity to the three explanatory variables, at the plot level, total herb species richness was positively related to the elevational factors summarized by the PC1 axis, and no relations with annual mean precipitation and precipitation of driest month (Fig. 3). The transect level showed a significant positive relation with the PC1 axis and negative relation with mean annual precipitation (Fig. S1). The species richness of ferns at the plot levels was significantly positively related to temperature (PC1 axis), while at the transect level was slightly related to precipitation of the driest month. The species richness of monocots at the plot and transect levels were not related to any of the factors included in our analysis. Finally, for dicots at plot levels we found a significant positive relationship with the PC1 axis, while for the other two factors

Table 2 Standardized partial regression coefficients of traditional ordinary least squared (OLS) regressions and simultaneous spatial autoregressive error (SAR) models with mean species richness per plot as response variable, and four environmental variables as predictor variables

	All species		Ferns		Dicotyledons		Monocotyledons	
Variables	OLS	SAR	OLS	SAR	OLS	SAR	OLS	SAR
Annual precipitation (mm)	–	–	0.25**	0.32**	– 0.29**	– 0.29**	−0.27*	–
Precipitation of driest month (mm)	0.43**	–	0.30**	–	–	–	0.57***	0.51***
PC1	0.66***	0.627***	0.80***	0.74***	0.35***	0.35***	–	–
Continent	–	–	0.37*	–	– 0.69**	– 0.69**	0.67***	072*
r^2	0.37***	0.38	0.62***	0.65*	0.44***	0.44	0.36***	0.43*
AIC	430	431	330	327	239	241	329	324
Delta AIC	2	3	0	1	0	1	1	2
Moran's I	0.03	0.00	0.12**	0.00	0.00	0.00	0.16***	−0.01

Minimal adequate OLS models were chosen from the best fitting model based on the Akaike information criterion (AIC). The lower spatial autocorrelation of errors in the SAR model confirm that there is no spatial autocorrelation among the plots left in the analyses. ΔAIC indicates the difference between the AIC of the model of interest and the AIC of the best fitting model. Moran's *I* has been used to assessed spatial autocorrelation in model residuals which can be considered a spatial equivalent to Pearson's correlation coefficient and normally varies between 1 (positive autocorrelation) and −1 (negative autocorrelation)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

the relationship was negative. At transect level, dicots species richness was negatively related to the mean annual precipitation and precipitation of the driest month. Beta diversity did not show any significant relationships for all the three groups with the PC1 axis, but weakly significant ones were recovered to mean annual precipitation (negative) for all the herbaceous species, ferns, and dicots. By contrast, ferns were significantly correlated (positively) to the precipitation of driest month (Fig. S2).

The multiple regression model for the total number of species at the plot and transect levels recovered only the PC1 axis to be strongly informative (Table 2). Beta diversity was only accounted for by mean annual precipitation (Table S1). The model for fern richness at the plot, transect, and beta levels included all the four factors with different values of statistical significance (Tables 2 and S1). The species richness of monocots was explained significantly by mean annual precipitation, precipitation of driest month and continents, at the plot transect and beta diversity level. Dicots species richness was related to mean annual precipitation, the PC1 axis, and continent at plot and transect level. Beta diversity for dicot species richness was significantly related to mean annual precipitation and continents.

The parallel analyses taking into account spatial autocorrelation resulted in roughly similar models (Table 2). Overall, spatial autocorrelation was almost fully accounted for in this series of analyses and most SAR models had lower AIC values than their respective OLS counterparts. There were no purely spatial patterns in the diversity data, suggesting that the diversity-environment relationships found by us are not spuriously driven by spatial autocorrelation.

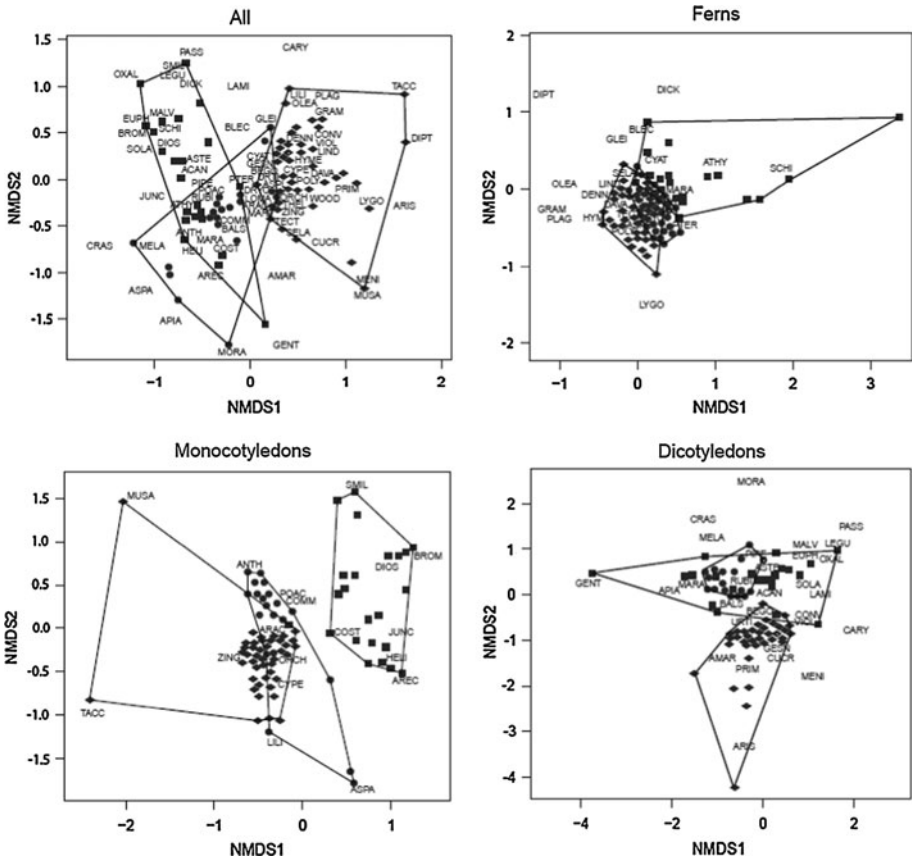

Fig. 4 Non-metric multidimensional scaling of families including all herbs as well as subsets of ferns, monocots and dicots found in our study transects in relation to the transect areas. *Squares* America; *circles* Africa; *rhombs* Asia

The non-metric multi-dimensional scaling analysis (NMDS) showed that at the family level herb assemblages from the Asian study sites were clearly separated from the African and American ones, while the latter two continents strongly overlapped (Fig. 4). Ferns showed overlaps between all three continents with the American transects slightly separated from those in Africa and Asia. Monocots similarly showed a separation of the American transects but also with only partial overlap of the African and Asian transects. Dicots revealed an even clearer separation of the Asian and Africa transects, with the latter overlapping with the American ones. The indicator species analysis recovered that America had 12 families that were significantly better represented there (1 fern, 7 monocot, and 4 dicot families), Africa had 11 characteristic families (4 ferns, 4 monocots, 3 dicots), and Asia had 16 such families (7 ferns, 3 monocots, 6 dicots) (Table 3).

Discussion

Let us first consider how the location of our study sites may have affected our results. First, despite including 23 widely scattered study sites, there are extensive tropical regions not

Table 3 Results of the indicator species analysis for the 72 families found in the study transects

America	Africa	Asia
Acanthaceae***	Agavaceae**	Araceae**
Arecaceae**	Aspleniaceae*	Convolvulaceae***
Bromeliaceae**	Balsaminaceae***	Cucurbitaceae***
Costaceae**	Commelinaceae**	Cyperaceae**
Dioscoridaceae**	Marantaceae**	Davalliaceae*
Euphorbiaceae***	Piperaceae***	Gesneriaceae ***
Heliconiaceae**	Poaceae**	Hymenophyllaceae*
Juncaceae**	Pteridaceae*	Lindseaceae*
Malvaceae***	Rubiaceae***	Lygodiaceae*
Schizaeaceae*	Tectariaceae*	Plagiogyriaceae*
Smilacaceae**	Woodsiaceae*	Polypodiaceae*
Solanaceae ***		Primulaceae***
		Selaginellaceae*
		Urticaceae***
		Violaceae***
		Zingiberaceae**

Families listed are significantly better represented in the transects of the respective continent than in those of the other two continents

* Ferns

** Monocots

*** Dicots

covered by us. Accordingly, although we compare sites on different continents, these need not be representative of the tropical rain forests on these continents as a whole. Thus, in the following text we explicitly refer, e.g., to our "African study sites" rather than to "Africa" as such. On the other hand, studies from additional sites may use our survey as a benchmark against which to assess regional differences in species richness. A further complication may arise from the inclusion of island floras in some of the "continents". This may be especially problematic for the isolated oceanic island of La Réunion that was colonized by plants via long-distance dispersal and may have a biogeographically unbalanced flora (Kreft and Jetz 2007; Kreft et al. 2010). Yet, the exclusion of this location from the African sites does not markedly affect our results (data not shown). In South East Asia, most of our sites are located on islands. However, these islands are all located on continental shelves. The Sulawesi Island has been isolated for most of its geological past and is situated far from both the Asiatic as well as the Australian mainland. But at the same time it is at cross-roads between the Sunda Shelf (Java, Sumatra, Borneo) in the west and the Sahul Shelf (New Guinea) in the east (Whitmore 1991). Furthermore, our sites in this region are located on both sides of Wallace's line, the major biogeographical boundary of the region (Wallace 1881; van Steenis 1950; Roos et al. 2004). We thus consider that our sampling is reasonably representative for the Malay region.

In our survey, we found that patterns of species richness at the plot and transect levels were highly concordant and are hence in the following treated together as "species richness". The range of 5–73 species of terrestrial herbs per transect found in this study shows that at this spatial grain the local species richness of understory herbs in tropical forest varies by about an order of magnitude. Understory herbs in tropical forest have previously been studied for each continent (e.g., Poulsen and Balslev 1991; Kelly et al. 1994; Poulsen and Pendry 1995; Annaselvan and Parthasarathy 1999; Chittibabu and Parthsarathy 2000; Costa 2004; Costa et al. 2005; Poulsen et al. 2005, 2006; Linares-Palomino et al. 2009) but we cannot directly compare these studies with our species number because they used different sampling techniques (contiguous versus non-contiguous plots, various plot and

transect shapes, different definitions of the herbaceous life form) and plot sizes (25–10,000 m^2).

The variation of the local species richness of understory herbs had a pronounced relationship with the environmental factors, with the models accounting for 21–73 % of the variation of species richness between transects. Climatic factors such as temperature are strongly correlated with elevation and were therefore combined in the PC1 axis which includes elevation along with related factors such as temperature and AET. The relative influence of these factors can therefore not be separated in our study.

Overall, we found that understory herb species richness at our study sites increased with elevation (PC1 axis) but showed no close relationship to precipitation values (Fig. 3). The first of these patterns is in accordance with numerous previous studies showing that the diversity of many groups of organisms increases in tropical mountains from the lowlands to some mid-elevation peak (Kessler et al. 2001, 2011; Rahbek 2005; Grytnes and Beaman 2006; McCain 2007, 2009) although other patterns are also often found, depending on taxon, elevational extent of the gradient, and sampling method (Rahbek 2005). The reasons for this increase are still poorly understood but presumably involve both the influence of higher humidity in mountains (Bhattarai et al. 2004; Kessler et al. 2011) as well as evolutionary legacies (McCain 2009; Kozak and Wiens 2010). The increasing herb diversity in the elevational range of 50–2,300 m found by us further suggests that along more extensive tropical elevational gradients (to above 3,000 m), herb species richness will overall show a hump-shaped elevational richness pattern since herb diversity is well known to decline near to and above the treeline (Wesche et al. 2008). This pattern is fundamentally different from the typical monotonic decline of species richness found in trees (Gentry 1988; Grytnes and Beaman 2006) and shows that different plant life forms respond differently to environmental factors.

The increase of plant species richness with water availability is well documented at local and regional scales (Gentry 1988; Kreft and Jetz 2007; Kreft et al. 2010). In our study, the lack of a relationship of richness of understory herb assemblages and water-related factors is unexpected. However, our survey only covered, with the exception of two Bolivian sites, evergreen tropical rain forests and most sites had values of mean annual precipitation well over 1,000 m. Accordingly, water may not be strongly limiting for herbs in these environment. If the study was extended to extra drought-deciduous forests or even desertic habitats, we would undoubtedly have found a strong relationship of herb diversity to water availability. Furthermore, there was a negative correlation of mean annual precipitation with elevation ($r = -0.41$).

Therefore, the herb diversity relationship between elevation and precipitation, positively and slightly negative respectively, is likely to be spurious. Indeed, although precipitation typically decreases with elevation, environmental humidity tends to increase because lower temperature reduce evaporation and because clouds and mist lead to further water input that is not accounted for by standard precipitation measurements (Gehrig Downie et al. 2011; Karger et al. 2012). More generally, understory plants are undoubtedly more directly influenced by microclimatic conditions than by the macroclimatic parameters considered by us (Wang et al. 2009). However, the forests microclimate is to large degree determined by forest structure (Lowman and Schowalter 2012) which in turn depends on macroclimate (along with other factors such as topography or disturbances). Thus, because our study only considered understory herb assemblages from mature forests, it is valid to consider the potential influence of macroclimatic parameters on understory plants, even if the inclusion of microclimatic data would certainly be desirable.

More distinct patterns become evident if we assess the major plant groups independently. This is analogous to the concept of "family-level niches" among tropical rain forest trees (Gentry 1988; Ricklefs and Renner 2012).

Ferns, which contributed 33 % to the herb species at our American sites, 42 % at the African ones, and 50 % at the Asian ones, tended to show more pronounced richness-environment relationships than the other groups. Ferns are well-known to show hump-shaped elevational richness patterns (Bhattarai et al. 2004; Kluge et al. 2006; Kessler et al. 2011) and to show strong richness-relationships to precipitation and air humidity (Soria-Auza and Kessler 2008). At the global scale, the diversity of ferns declines more strongly towards arid and cold habitats than that of angiosperms (Kreft et al. 2010) suggesting that fern species richness are more strongly constrained by extreme climatic conditions. The same trends were seen in our study, although the relationship to elevation overrode that to precipitation, presumably for the same reasons as detailed above for overall herb diversity.

Dicots, which contributed 41 % of the species at the American sites, 33 % at the African ones and 35 % at the Asian ones, showed patterns that parallel those of all herbs and ferns, but showed more marked decreases of diversity with increasing precipitation. This pattern contradicts the commonly seen increase of angiosperm diversity with increasing water availability (Gentry 1988; Kreft and Jetz 2007; Kreft et al. 2010), but again it has to be kept in mind that our survey only covered tropical rain forests and that precipitation and elevation were correlated. In any case, it is likely that the combination of the contrasting patterns probably leads to the lack of a pattern for overall herb richness, as previously documented for herb richness along an elevational gradient (Willinghöfer et al. 2012).

Monocots, which contributed 26 % of the species at the American sites, 25 % at the African ones and 17 % at the Asian ones, differed markedly from the previous groups in showing poorly defined richness-environment relationships overall and having higher diversity especially in warmer as well as to some degree in higher and seasonally less arid habitats. This interesting result reflects the high abundance and diversity of monocot herbs in lowland forests, both in humid ones where they are best represented by members of the Zingiberales (Costaceae, Heliconiaceae, Marantaceae, Zingiberaceae, etc.) (Larsen et al. 1998) and the family Araceae (Mayo et al. 1997, 1998) as well as in dry ones where grasses (Poaceae) predominate.

The different richness and the relationship with environmental factors between the three major plant groups presumably reflect their evolutionary history and their physiological tolerances and adaptation strategy. There is increasing evidence that ferns are less capable of optimizing their water-use efficiency than angiosperms (Brodribb and Holbrook 2004; Brodribb et al. 2009; MacAdam and Brodribb 2012) while at the same time having more sensitive photoreceptors (Schneider et al. 2004). This appears to concentrate ferns in more shady and humid environments than angiosperms. Many monocot families, on the other hand, have originated in the tropics and have had only limited success in adapting to low temperatures, especially frost (Marquez et al. 2006).

Beta diversity was measured by us as the ratio between the total number of species from a transect to the mean number of species per plot. Although a priori one might expect that this ratio might vary considerably, e.g., if species show more patchy distributions under certain environmental conditions, we essentially found no systematic variation in beta diversity (Table S1; Fig. S2). Indeed, species richness at plot and transect scales were closely correlated, showing that they reflected the same overall diversity patterns (Fig. S2). At different spatial scales, beta diversity may well show regional differences, as shown, for example, for trees in tropical America (Pitman et al. 2008).

Comparing the understory herb assemblages sampled on the different continents, we found no significant differences in the richness of the overall herb assemblages. The relevant result is that the contribution of the different taxonomic groups to the richness of our study sites differed between continents, with American sites being dominated by dicots whereas ferns were the most species rich group at the Asian sites and African with the least reach site. This suggests that there might be continental deviations in the relative contribution of the three major taxonomic groups. The limitation of the sampled localities imply that a careful consideration has to be taken when reaching conclusions, but it is striking that the different patterns of species richness between taxonomic groups counterbalance each other, so that overall we found no difference in herb species richness between continents. While a correlative study such as ours cannot directly inform about processes determining local species richness, the above pattern might suggest that the local species richness of tropical herbs is limited by the number of species that can co-occur locally, but that the taxonomic composition may shift, either due to ecological differences between the taxa or as a result of historical factors (Mark 2002; Ricklefs and Renner 2012). This intriguing hypothesis may be subjected to experimental studies.

Although almost all families found in our study have pantropical distributions (the main exceptions being American Bromeliaceae and Heliconiaceae), sites on different continents were characterized by different understory plant families (Table 3). Monocot families such as Taccaceae, Musaceae, and Zingiberaceae, all of which have an Asian centre of diversity, were not recovered as significant in the indicator species analysis, probably because they either also occurred in Africa (Zingiberaceae) or were too rarely recorded in the Asian transects. Among the dicots, American and African sites shared many families while Asian transects were characterized by a set of distinct families. The indicator species analysis recovered the presence of eight fern families representative for the sites on the three continents (4 in Asia, 3 in Africa, 1 in America) highlighting that the family distribution and richness may be related to factors not included in this study. Previous biogeographical studies on ferns have suggested that most of the current fern diversity evolved after the rise of angiosperms to ecological dominance through a series of successive replacement events (Schneider et al. 2004). Most of the modern angiosperm families also originated after the fragmentation of the supercontinent Gondwana (Burnham and Johnson 2004; Davis et al. 2005) leading to continent-specific radiations (Corlett and Primack 2006).

In conclusion, we found that environmental and geographical factors account for a large proportion of the variation in the local species richness of tropical forest herbs and that, when all herbs were analysed in combination, there were few environmental patterns and no differences in diversity between the continents. However, when we separated the different taxonomic groups (ferns, monocots, dicots) we found markedly different patterns relative to environmental factors. Furthermore, significant results show that continents were characterized by distinct sets of families. These results prompt us to ask: which factors ultimately determine the local richness of tropical herb assemblages? Assemblages may either be saturated so that the ecologically possible numbers of species as determined by resource availability or heterogeneity actually co-occur. Alternatively, the number of species at different sites may be constrained by evolutionary or historical processes, involving different times since origination or colonization or differences in speciation or extinction rates (Wiens and Donoghue 2004; Jablonski 2008). The overall patterns found by us result from the addition of distinct patterns at the family and group level, suggesting that the first of these alternatives may apply. Testing this hypothesis will require experimental studies to determine if tropical herb assemblages are indeed saturated as well as detailed dated phylogenetic trees to assess the evolutionary history of these assemblages.

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